# Larval and pelagic juvenile fishes collected with three types of gear in Gulf Stream and shelf waters in Onslow Bay, North Carolina, and comments on ichthyoplankton distribution and hydrography\*

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The fish fauna in waters off North Carolina is diverse, receiving contributions from the Virginian, Carolinian, and Caribbean faunal provinces (Gray et al., 1968; Schwartz, 1989). South of Cape Hatteras exist livebottom habitats, small areas of rock outcroppings containing rich sessile invertebrate communities and many species of commercially and recreationally important subtropical and tropical fishes (Huntsman, 1976; Miller and Richards, 1979). Little is known about the patterns and source of recruitment of many of these and other fishes. Fahay (1975) sampled a transect off New River Inlet, North Carolina, and Cape Fear, North Carlina, at quarterly intervals with a surface-towed meter net. Eldridge et al. (1978) examined the performance of a 2 m  $\times$  1 m neuston net

in waters off South Carolina. Powles and Stender (1976) surveyed ichthyoplankton from Cape Fear, North Carlina, to Cape Canaveral, Florida, with a standard ichthyoplankton bongo sampler. Ichthyoplankton research targeting live-bottom habitats in Onslow Bay, North Carlina, was recently conducted by Powell and Robbins (1998), who provided information on spatial and temporal spawning. The use of standard ichthyoplankton samplers, however, may introduce bias against the capture of late-larvae and early-juveniles owing to net avoidance (Shima and Bailey, 1994); therefore little information would be gained about recruitment sources and patterns.

The use of complementary gear that could collect a series of pelagic larval stages would be useful in understanding the source of recruits to live-bottom and other habitats off North Carolina. The spatial distributions of larval stages could indicate if recruitment is from local populations, or other sources, (Leis, 1994; Booth and Brosnan, 1995). However, the spatial distribution of larval stages needs to be coupled with oceanographic observations to interpret the source of recruits.

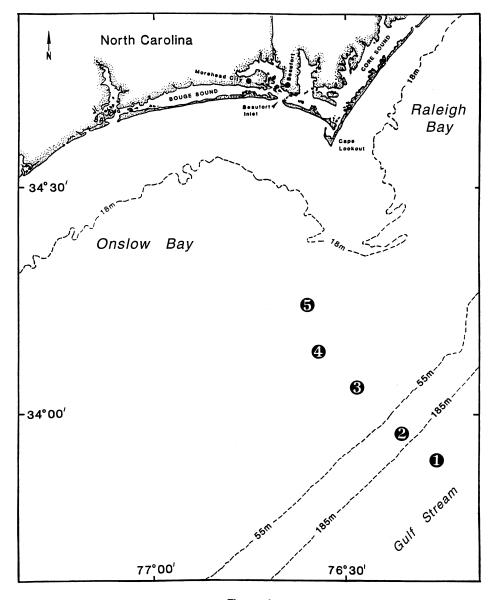
The major goal of our study was 1) to examine the effectiveness of three gear types in collecting a complete series of the pelagic larval phase of reef fishes and associated taxa, and 2) to examine the influence of short-term hydrographic conditions on fish distributions.

#### Materials and methods

Sampling was generally conducted in darkness aboard the RV Cape Hatteras, 14–16 September 1994, along an onshore-offshore transect in Onslow Bay (Table 1, Fig. 1). With some modifications, we followed Struhsaker (1969) in classifying habitat types: coastal (<18 m); middle-shelf (18-55 m); outer-shelf (55–185 m); and oceanic (>185 m). Station 1 (76°15.0′W, 33°54.0′N) was located in oceanic waters (water depth=341 m); station 2 (76°21.3'W, 33°58.5'N) was located in outer-shelf waters where smooth to highly broken bottom exists (water depth= 75–110 m); station 3 (76°27.8'W, 34°04.0'N) was located in middleshelf waters (water depth=40 m); and stations 4 (76°34.2'W, 34°08.7'N) and 5 (76°35.5'W, 34°14.3'N) were located on the middle shelf adjacent to live-bottom habitat (water depth=33-35 m and 28-31 m, re-

Manuscript accepted 8 November 1999. Fish. Bull. 98:427–438 (2000).

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**Figure 1** Location of sampling stations.

spectively). Stations 1 and 2 were influenced by the Gulf Stream.

Three samplers were used: a 60-cm diameter bongo sampler with 0.333-mm mesh nets, a 5-m² Methot frame trawl with 2×3 mm oval mesh (Methot, 1986), and a 1×2 m neuston net with 0.947-mm mesh. The bongo sampler was towed obliquely at 1.5 knots for a minimum of 5 min to insure 150 m³ of water was sampled. The Methot frame trawl was towed obliquely at 4 knots for a minimum of 20 min to insure that >10,000 m³ of water had been sampled, except for one tow of 10 min on 14 September 1994 at station 2 at 2111 hours. Both the bongo sampler and frame trawl were retrieved in a modified step oblique tow after deployment to a depth approxi-

mately 10 m from the bottom, except at station 1 where nets were deployed to a maximum depth of 170 m. The neuston net was towed for 10 min at 1.5 knots with approximately one-half of the net under water. Volume estimates for bongo nets and Methot frame trawl were based on General Oceanics flowmeter readings. No volume readings were taken for neuston tows. A summary of sample data is presented in Table 1. Samples were preserved in 95% ethyl alcohol. Body length measurements are notochord lengths (preflexion and flexion stages) or standard lengths (postflexion and juvenile stages).

At each station a conductivity-temperature-depth (CTD) probe (Sea-Bird model 911plus) was cast to within 1–3 m of the bottom. Temperature and salin-

#### Table 1

Summary of sample data taken in waters off North Carolina. For gear type: frame =  $5 \text{ m}^2\text{-Methot frame trawl}$ with 3×4 mm oval mesh (Methot, 1986); bongo = 60-cm bongo nets with 0.333-mm mesh; neuston =  $1\times2$  m neuston net with 0.947-mm mesh. Density of larvae indicates numbers/100 m<sup>3</sup> for bongo nets; numbers/10,000 m<sup>3</sup> for frame trawl; and numbers/10-min tow for neuston net.

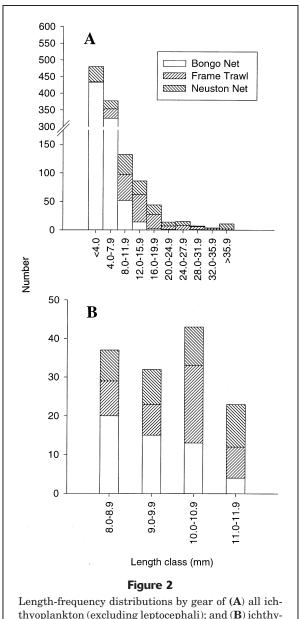
Date	Station	Time	Gear	Density of larvae
14 Sep 1994	2	2111	frame	27
		2149	frame	29
		2244	bongo	112
		2307	neuston	32
15 Sep 1994	3	0122	frame	15
		0204	bongo	79
		0224	neuston	33
	4	0401	frame	25
		0445	neuston	29
		0458	bongo	72
	5	0620	frame	3
	1	2108	frame	9
		2148	bongo	26
		2207	neuston	23
16 Sep 1994	2	2341	frame	16
		0024	neuston	26
		0040	bongo	82
	3	0201	frame	8
		0235	bongo	161
		0244	neuston	20
	4	0355	frame	23
		0427	neuston	58
		0443	bongo	156
	5	0541	frame	19
		0616	bongo	118
		0625	neuston	29

ity measurements were reviewed for aberrant data points. Satellite-derived advanced very high resolution radiometer (AVHRR) data (NOAA/NESDIS Coast-Watch node, NMFS Beaufort Laboratory) were used to examine sea surface temperature (SST) during the study period (1–20 September 1994). A nonparametric Kruskal-Wallis test (SAS Institute, Inc., 1987) was used to evaluate differences in fish lengths between gear types, and between days at specific stations.

## Results

#### Larval length distributions by gear

There was a significant difference in length of larvae among gears (Kruskal-Wallace Test, P < 0.01). The



thyoplankton (excluding leptocephali); and (B) ichthyoplankton between 8.0 and 12.0 mm in length.

neuston net and frame trawl collected larger larvae, whereas the bongo net collected smaller larvae (Fig. 2A). The bongo net was more effective in collecting larvae <10.0 mm, and the frame trawl and neuston net were more effective in collecting larvae 10.0 mm (Fig. 2B). A wide range of size classes was obtained with the neuston net and frame trawl, but catches typically were low (Table 1, Fig. 2).

Some 40 reef fish taxa were collected (Table 2); approximately 25 with the bongo sampler, 24 with the frame trawl, and 14 with the neuston net. Five families were commonly collected (Table 3), but a size series of only two taxa (Acanthurus sp(p), and

Table 2

The frequency of occurrence from n samples and, in parenthesis, the density (bongo net=numbers/100 m³, frame trawl=numbers/10,000 m³, neuston net=numbers/10-min tow: summed over all stations) of reef-associated taxa collected with three different samplers in September, 1995, in waters off North Carolina.

Family	Taxa	Bongo net $(n=10)$	Frame trawl $(n=8)$	Neuston net $(n=8)$
Acanthuridae	Acanthurus bahianus		2(4.0)	
	A. bahianus/chirurgus		1(0.8)	
	A. chirurgus		1(1.1)	
	A. coeruleus	1 (0.8)	1(1.1)	
	$A can thurus \ { m sp}({ m p}).$	1 (0.8)	2(1.4)	2(2.0)
Balistidae	$Balistes\ capriscus$		1(0.6)	2(2.0)
	unidentified	3 (2.0)	1(0.6)	1(1.0)
Carangidae	Alectis ciliaris		1(0.8)	
	$Seriola \ sp(p).$	1 (1.3)	1(0.6)	1(2.0)
Chaetodontidae	$Chaetodon\ ocellatus$		1(0.6)	
Diodontidae	unidentified		1(0.8)	
Fistularidae	Fistularia sp(p).	1 (1.5)	1(0.8)	
Gobiidae	Ioglossus calliurus	3 (2.8)		
Holocentridae	unidentified	2 (1.0)	2(1.3)	3(3.0)
Labridae	Bodianus sp.	1 (0.6)		
	$Halichoeres \ { m sp}({ m p}).$	2 (5.5)		
Lutjanidae	$Etelis\ oculatus$	1 (0.5)		
	$Lut janus\ campechanus$	1 (0.7)		
	$Pristipo moides\ aquilonaris$	1(0.7)		
	Rhomboplites aurorubens	5(11.7)		1(1.0)
	unidentified	4(15.2)		
Monacanthidae	Aluterus scriptus		1(0.8)	
	Aluterus sp.		1(0.8)	
	Cantherines sp. Monacanthus ciliatus		1(0.6) $3(2.2)$	
	Monacantnus cittatus M. hispidus	1 (1.3)	3(2.2) $4(4.4)$	2(6.0)
Muraenidae	Gymnothorax moringa	_ (=.0)	1(0.6)	_(313)
Maracinac	G. ocellatus complex		3(5.5)	
	Gymnothorax sp(p).	1 (1.3)	1(1.5)	
	unidentified	1 (1.3)		1(1.0)
Ogcocephalidae	unidentified	1 (0.7)	2(2.2)	
Pomacanthidae	$Holacanthus\ { m sp}({ m p}).$	2 (4.0)		
	unidentified	1 (1.3)		
Pomacentridae	$Pomacentrus\ { m sp}({ m p}).$	3 (2.6)		
	unidentified	1 (0.7)		2(2.0)
Priacanthidae	Pristigenys alta	F (0.4)	1(0.9)	
a	unidentified	5 (8.4)	1(0.6)	_, .
Scaridae	type A	6(15.6)		2(7.0)
	type B	5 (9.8)		1(1.0)
a	unidentified	1 (1.5)	47E - 1	
Scorpaenidae	Scorpaena sp. unidentified	7 (9.0)	1(0.6)	1(2.0)
	umuemmeu	7 (3.0)		
				continue

Family	Taxa	Bongo net $(n=10)$	Frame trawl $(n=8)$	Neuston net (n=8)
Serranidae	Diplectrum formosum	2 (1.3)		
	Epinephelus cruenatus		1(1.7)	
	$E.\ niveatus/flavolimbatus$	1 (0.8)		
	$Hemanthias\ vivanus$			1(1.0)
	$Liopropoma \ sp(p).$			2(2.0)
	Rypticus sp(p).	2(1.3)		
	Serraninae type A	2(2.7)		
	Serranus sp.		1(0.6)	
	subfamily Serraninae	3(11.8)		
	tribe Epinephelini			1(1.0)
Syngnathidae	Hippocampus erectus		2(1.4)	3(3.0)

# Table 3

The range of body lengths, by gear, for the most commonly collected taxa, identified below the family level. Values in parentheses indicate the number of fish measured. Bongo = 60-cm bongo nets with 0.333-mm mesh; Frame = 5-m² Methot frame trawl with  $3\times4$  mm oval mesh; and Neuston =  $1\times2$  m neuston net with 0.947-mm mesh.

Taxa	Bongo net	Frame trawl	Neuston net	
Reef fish taxa				
Acanthuridae				
A can thur us sp(p).	2.5-8.6	4.7 - 10.2	3.0-3.3	
	(11)	(10)	(2)	
Labridae				
Halichoeres sp(p).	2.1 – 5.4	_	_	
	(8)			
Lutjanidae				
Rhomboplites aurorubens	2.9 – 5.6	_	4.2	
	(18)	_	(1)	
unidentified	1.9–3.4	_	_	
	(30)	_	_	
Priacanthidae				
Pristigenys alta	_	10.3		
		(1)		
unidentified	1.8-4.4	_	3.1-4.1	
	(19)	_	(4)	
Scaridae				
type A	2.9-7.7	_	8.4-9.8	
	(18)	_	(7)	
type B	2.7-7.7	_	7.6	
	(11)	<del>-</del>	(1)	
Pelagic taxa				
Carangidae				
Decapterus punctatus	2.1-14.7	18.7	2.9-11.0	
= 115pto. ao panetatao	(30)	(1)	(10)	
$Selar\ crumen oph thalmus$	3.7–6.7	7.3–16.2	4.1–5.0	
Seca. Commenopronamia	(5)	(16)	(2)	
	(3)	(20)	continue	

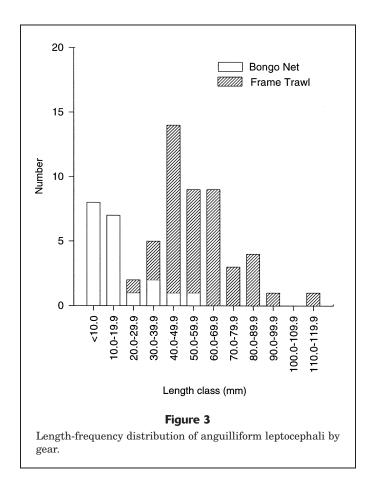
Table 3 (continued)					
Гаха	Bongo net	Frame trawl	Neuston net		
Coryphaenidae					
Coryphaena equisetus	4.4-4.6	_	10.0-19.2		
	(2)	_	(12)		
$C.\ hippurus$	_	_	12.3-43.0		
	_	_	(15)		
Scombridae					
Auxis sp(p).	2.6 - 7.1	10.7	4.0 - 18.3		
	(20)	(1)	(6)		
$Scomberomorus\ cavalla$	2.8-6.2	13.5	4.2 - 7.9		
	(38)	(1)	(4)		
Thunnus $sp(p)$ .	2.6-6.2	4.6 - 5.7	4.7 - 5.7		
	(12)	(2)	(14)		
Demersal taxa					
Bothidae					
Bothus sp(p).	2.0-15.0	6.5 - 19.5	3.4-6.0		
* **	(104)	(30)	(18)		
Trichopsetta ventralis	30.0	13.5–29.8	_		
•	(1)	(20)	_		
Callionymidae					
Diplogrammus pauciradiatus	1.2-3.4	_	_		
	(66)	_	_		
Paradiplogrammus bairdi	1.7-6.2	_	3.5-6.0		
	(9)	_	(6)		
Caproidae					
Antigonia sp(p).	2.8-6.3	3.4-8.3	2.7 - 4.0		
	(16)	(6)	(2)		
Labridae					
Xyrichtys novacula	2.4 - 9.9	6.2	6.8 - 13.5		
	(46)	(1)	(2)		
Ophididae					
$Ophidion\ selenops$	1.9-16.0	_	_		
	(8)	_	_		
$Otophidion\ omostigmum$	3.1-8.3	_	_		
	(14)	_	_		
Paralichthyidae					
$Syacium\ papillosum$	1.3-12.7	4.2-9.3	3.2 - 4.3		
	(92)	(3)	(25)		

Scaridae type A) were collected with complementary gear. The bongo sampler and frame trawl were effective in collecting a series of  $Acanthurus\ sp(p)$ , the bongo and neuston net in collecting Scaridae type A. Larvae of the economically important  $Rhomboplites\ aurorubens$  were collected almost exclusively with bongo nets and ranged from 2.9 to 5.6 mm (Tables 2 and 3). The unidentified lutjanid larvae were probably  $R.\ aurorubens$  because few  $Lutjanus\ campechanus\ were\ collected\ (n=3)$ .

Of the seven commonly collected pelagic taxa, size series of four taxa (Selar crumenophthalmus, Coryphaena equisetus, Auxis sp(p)., and Scomberomorus

cavalla) were collected with complementary gear (Table 3). Except *S. crumenophthalmus*, which was effectively collected with the bongo sampler and frame trawl, all others were collected with the bongo sampler and neuston net. *Coryphaena hippurus* specimens were large and collected solely with the neuston net.

The frame trawl effectively sampled large anguilliform leptocephali, and the bongo sampler was a good complementary gear for collecting smaller specimens (Fig. 3). Only one leptocephalus was captured with the neuston net. Taxa representing three families were collected: Congridae (*Ariosoma balearicum*, *Bathycongrus* sp(p)., *Heteroconger luteolus*, *Para-*



conger caudilimbatus); Muraenidae (Gymnothorax moringa, G. ocellatus complex); and Ophichthidae (Callechelys muraena, Gordiichthys ergodes, Letharchus aliculatus, Ophichthus gomesii, O. melanoporus, O. puncticeps).

A size series of two demersal species (*Bothus* sp(p). and *Antigonia* sp(p).) was collected with the bongo net and frame trawl (Table 3). Because size of *Bothus* at metamorphosis is approximately 16–21 mm (Fahay, 1983), our collections represent a complete size series. Species most likely include *B. ocellatus* and *B. robinsi* (Robins and Ray, 1986), both of which inhabit middleshelf waters as adults (Schwartz, 1989). The series of antigonids did not include the large pelagic stage (ca. 13–14 mm). All the specimens that had developed meristic characters (ca. 5.0 mm) were *Antigonia capros*. On this basis, the smaller specimens might be *A. capros*, but *A. capros* and *A. combatia* exist sympatrically in the western North Atlantic (Berry, 1959).

#### Hydrography and ichthyoplankton distribution

A major hydrographic feature observed in SST imagery was a large frontal eddy that was propagating northeastward and associated with a Gulf Stream meander crest (Fig. 4). A warm filament of Gulf Stream derived water lay over the shelf and resulted from the cyclonic circulation of the frontal eddy. This filament was bounded inshore by cooler shelf water and separated from the Gulf Stream by cooler water of the frontal eddy.

Temperature and salinity were in concordance with the SST imagery (Fig. 5). On 15 September 1994 (day 1), domed-shaped isotherms and lower salinities were observed at station 2 indicating recent upwelling from the passage of the frontal eddy (Fig. 4). The warmer and more saline water on the shelf on day-1 (Fig. 5) was consistent with the presence of stranded Gulf Stream water resulting from the frontal eddy filament observed on the SST imagery (Fig. 4). Associated with this stranded Gulf Stream water on the middle-shelf was a diverse group of larvae that are not known to occur as adults or spawn in middle-shelf waters (Table 4). The frequency occur-

<sup>&</sup>lt;sup>1</sup> Richards, W. J. 1991. National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia drive, Miami, FL 33149. Unpubl. data.

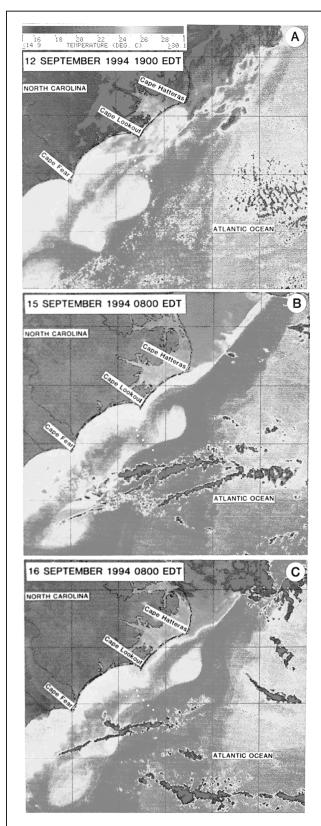


Figure 4

Sea-surface-temperature satellite imagery during (A) 12 and, (B) 15 and, (C) 16 September 1994 off North Carolina. Station locations are referenced. See Figure 1 for station numbers.

rence of these larvae appeared to be similar on both days as was the presence of Gulf Stream water.

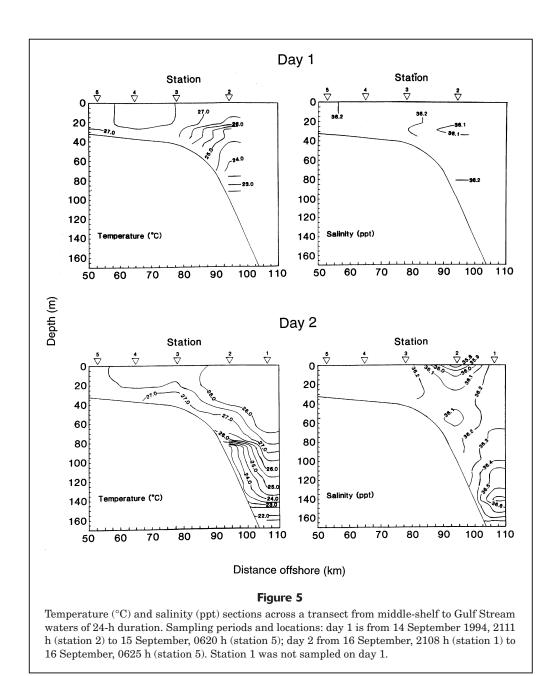
On 16 September 1994 (day 2), hydrographic conditions had changed markedly offshore (Fig. 5). At the surface of station 2, warm, low-salinity water was present, indicating water of coastal origin. But the temperature was higher than observed over the Carolina shelf in the SST imagery (Fig. 4), indicating a more southern coastal origin for this water. Accompanying these changes in outer-shelf waters, the length-frequency distributions of the two most abundant taxa, *Bothus* sp(p). and *S. papillosum*, differed significantly between day 1 and day 2 (Kruskal-Wallace Test; P<0.01 for both taxa). Very small larvae of both middle-shelf taxa were abundant in outershelf waters on day 2 but absent on day 1 (Fig. 6).

# **Discussion**

#### **Gear comparison**

A series of pelagic larvae and juveniles was collected with complementary gear for Acanthurus sp(p)., Antigonia sp(p)., Bothus sp(p)., Scaridae type A, and Selar crumenophthalmus. The Methot frame trawl was not successful in collecting large larvae or early juveniles of economically important reef fish species (snappers and groupers), probably due to the low abundance of adult populations. In other studies, the frame trawl has successfully collected large larvae and juveniles of those species whose adults are extremely abundant (i.e. Theragra chalcogramma [Shima and Bailey, 1994; Brodeur et al., 1995]) and Engraulis mordax, [Methot, 1986]). Economically important reef fish species are relatively rare and larger size pelagic larvae and juveniles are rarer than young larvae. Longer frame-trawl tow times (one hour) will be required, but this would limit the extent of the area to be sampled and decrease the quality of the specimens. The bongo sampler is generally limited in its ability to collect late-stage larvae or early pelagic juveniles owing to net avoidance (Shima and Bailey, 1994); however, it is a more effective sampler than either the neuston net or frame trawl in collecting early stage larvae, and it is needed to obtain information on spatial and temporal spawning.

The frame trawl is effective in capturing leptocephali, and because the leptocephalus is a true oceanic form regardless of habitat as an adult (Smith, 1989), it is a valuable indicator species in studies dealing with cross-shelf transport. Similarly, the frame trawl is effective in capturing *Trichopsetta ventralis*, a resident of the Gulf of Mexico (Robins



and Ray, 1986) and an indicator that certain larvae spawned in the Gulf of Mexico as well as other organisms (Pietrafesa, 1989) can be transported to shelf waters off North Carolina.

Our study and previous studies (Eldridge et al., 1978) indicate that the 1 m  $\times$  2 m neuston net is as effective in sampling large larvae and juveniles as is the frame trawl, although a comparison has not been made by using both nets as neuston nets. Eldridge et al. made a large number of neuston tows (24 day, 24 night) and, in some cases, collected larger fishes (e.g. Decapterus sp,  $Selar\ crumenopthalmus$  and Priacan

thidae). However, they did not collect any Acanthuridae, *Trichopsetta*, and *Antigonia* sp(p)., taxa that were relatively common in frame trawl collections. A comparison between the two gear types for neuston tows could be informative.

# Ichthyoplankton distribution in relation to hydrography

Factors influencing the hydrography of the waters off North Carolina are complex and dynamic (Pietrafesa, 1989; Pomeroy et al., 1993; Verity et al., 1993) and

Table 4

The occurrence of larvae (denoted by a "+" sign) from taxa that occur or spawn as adults in oceanic (>185 m) and outer-shelf waters (55–185 m) or that occur south of the study area (denoted by an asterisk) collected in middle-shelf waters (stations 3 and 4) during two sampling periods of 24-h duration (denoted by day 1 and day 2).

Family	Species	Day 1	Day 2	Family	Species	Day 1	Day 2
Acropomatidae	Synagrops sp.		+	Lutjanidae	Etelis oculatus*		+
Balistidae	$Can thidermis\ maculatus$	+		Muraenidae	Gymnothorax ocellatus comp	lex+	
Bathypteroidae	unidentified		+			+	
Bothidae	$Trichopsetta\ ventralis^*$	+	+		unidentified		+
Caproidae	Antigonia capros (?)	+	+	Myctophidae	$Benthosema\ suborbitale$	+	
Carapidae	$Carapus\ bermudensis^*$		+		Ceratos copelus sp(p).	+	+
Chiasmodontidae	unidentified		+		$Notolychnus\ vald$ iviae		+
Congridae	Ariosoma balearicum	+	+		unidentified	+	+
	Bathycongrus sp(p).	+	+	Nomeidae	$Cubiceps\ paucira { m diatus}$	+	
	Heteroconger luteolis	+		Notosudidae	$Scope los aurus\ smithii$		+
	Paraconger caudilimbatus	3 +		Ophichthidae	$Gordiichthys\ er$ godes		+
Gempylidae	Gempylus serpens	+		Paralepididae	Lestidium atlanticum	+	
	Nesiarchus nasutus		+		unidentified	+	
Gonostomatidae	$Cyclothone \ { m sp}({ m p}).$	+	+	Paralichthyidae	Citharichthys gymnorhinus	* +	+
Lobotidae	$Lobotes\ surinamens is *$		+	Phosichthyidae		+	

certainly influence the composition of ichthyoplankton on the continental shelf. A major feature is the intrusion of Gulf Stream waters onto the continental shelf. Additionally, during summer, southwest winds result in the advection of shelf waters south of North Carolina onto the North Carolina shelf (Pietrafesa, 1989). Intrusions of the Gulf Stream, along with the advection of Georgian shelf water, appeared to be evident in our study and could have influenced the composition of ichthyoplankton on the shelf—particularly evident at the outer-shelf station (station 2) where hydrographic conditions and size composition of the two most abundant taxa changed within a 24-h period.

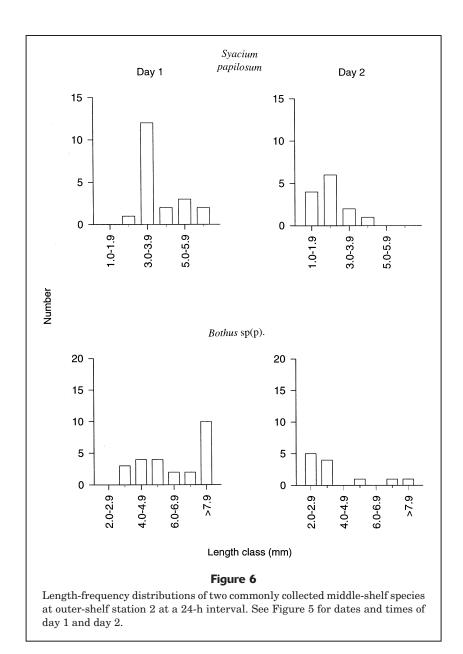
We identified 21 species of larvae on the middle shelf from oceanic and outer-shelf waters and five species which, as adults, occur in shelf waters south of the study area (Table 4). The intrusion of these larvae is a common event that occurs throughout all seasons (Powell and Robbins, 1994; 1998; our study) and appears to be related to water expelled from frontal eddies created by Gulf Stream meanders that have stranded on the continental shelf. Nevertheless, we were unable to determine the role of cross shelf transport in the recruitment of subtropical and tropical reef fishes and other taxa to waters off North Carolina.

Our observations on larval fish distribution patterns in relation to hydrography are derived from five stations over a 48-h period. Longer-term studies, with

extensive sampling, will be necessary to test assumptions made in our study, especially the transport of larvae from the middle shelf to the outer shelf. Syacium papillosum a middle-shelf species that is abundant from spring to early fall (Powell and Robbins 1994; 1998; our study) could serve as an indicator of transport in long-term studies. Such studies could test the hypothesis that circulation patterns during late spring, summer, and early fall in shelf waters off North Carolina retain larvae within the bays. The major goal of future research should be to develop a comprehensive model or scenario of larval transport based on circulation patterns (e.g. Hare and Cowen, 1996). Such a model could provide a lucid framework for testing larval transport hypotheses and be of heuristic value as new problems are discovered.

# Acknowledgments

We wish to express our appreciation to the crew of the RV *Cape Hatteras* and those individuals who participated in the cruise, especially Mike Greene. We especially thank David Smith and Mark Leiby for leptocephali identification, Curtis Lewis for figure preparation, and Dave Colby and Jim Waters for computer assistance. Comments by Bill Hettler, Patti Marraro, and Dave Peters along with those of two anonymous reviewers greatly improved the manuscript.



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